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Maximum Entropy Modeling of Indiana Bat (*Myotis Sodalis*) Maternity Roost Habitat

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**MAXIMUM ENTROPY MODELING OF INDIANA BAT (*MYOTIS SODALIS*)
MATERNITY ROOST HABITAT**

A Masters Thesis

Presented to

The Graduate College of
Missouri State University

In Partial Fulfillment

Of the Requirements for the Degree
Master of Science, Biology

By

Joseph R. Lemen

May 2015

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MAXIMUM ENTROPY MODELING OF INDIANA BAT (*MYOTIS SODALIS*) MATERNITY ROOST HABITAT

Biology Department

Missouri State University, May 2015

Master of Science

Joseph R. Lemen

ABSTRACT

Since 1967, the Indiana bat (*Myotis sodalis*) has been on the U.S. Endangered Species list due to disruption of hibernating bats in caves, summer habitat degradation, and more recently, the onset of White-nose Syndrome. The purpose of this study is to evaluate landscape variables associated with Indiana bat maternity roost trees in an attempt to better understand what factors play a role in their distribution in north central Missouri. I tracked reproductive female Indiana bats to 20 different primary and secondary roost trees; these are roosts that had multiple bats visit them on multiple occasions. GPS location data for these roosts and 6 environmental parameters (aspect, distance to forest edge, distance to stream or river, elevation, percent tree canopy, and slope) were used as input variables for a MaxEnt model of species distribution. I used ENMTTools to identify which analysis features produced the best MaxEnt model for this data set. Linear and quadratic analysis features, separately, fit the data the best. When cross-validated through four replicates, the two models performed equally well with area under the curve (AUC) values of 0.792 and 0.764. Distance to forest edge was the variable with the most influence in both models, followed by elevation and distance to stream. Macro-scale environmental variables provide insight to modeling areas in which Indiana bat maternity roosts might be found in the future. This provides researchers and wildlife managers with a toolset to identify potential habitat to aid in species recovery.

KEYWORDS: Indiana bat, *Myotis sodalis*, landscape, maternity roost, reproduction, MaxEnt

This abstract is approved as to form and content

Lynn W. Robbins, Ph.D.
Chairperson, Advisory Committee
Missouri State University

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ACKNOWLEDGEMENTS

I would like to thank Shannon Romeling, Ryan Allen, Larisa Bishop-Boros, Nathan Light, Tom Tomasi, Sean Maher, Kate Ramsey, Rebecca Ringling, Amanda Janicki, Cory Armstrong, Josh Paris, Eric Hufford, Shelly Colatske, Ron Colatske, Josh Flynn, J.T. Layne, Zack Holme, Jude Benavides and Anthony Reisinger for their support during the course of my graduate studies. These fine people endured countless hours of discussion and debate whether over the phone or while camping in the middle of nowhere for days on end. I would like to thank my friend and confidant Ben Hale for his unending enthusiasm and support throughout this process. Ben, I will always cherish the times we spent together in the field and on the road. Most of all, I want to thank my wonderful wife and research partner Janelle Lemen. From the first day I met you in Dr. Tomasi's lab, all I wanted to do was help you chase bats.

I dedicate this thesis to Lynn Robbins, a great mentor in every sense of the word.

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INTRODUCTION

Indiana Bat Life History

The Indiana bat (*Myotis sodalis*) is a relatively small vespertilionid bat, usually 5-10 g, found in eastern North America. The wingspan is generally 24-27 cm with a forearm length of 35-41 mm. Of all the *Myotis* species, Indiana bats most closely resemble the little brown bat (*Myotis lucifugus*; Barbour and Davis, 1969). While the two bats are morphologically similar, Indiana bats have a distinctly keeled calcar and generally smaller hind feet with shorter hairs that do not extend beyond the toes. The fur ranges from dark gray to grayish-brown and can be somewhat lighter on the chest and belly.

This species is known from New England south to portions of Alabama and west to Missouri, Iowa and northern Arkansas (USFWS, 2007). Indiana bats were listed as in danger of extinction under the Endangered Species Preservation Act of 1966, and are currently listed as endangered under the Endangered Species Act of 1973, as amended (USFWS, 2007). The original listing of the species can be attributed to a sharp decline in the population due to human disturbance of hibernating bats in the 1960s. Indiana bat hibernate in large numbers in just a few caves and therefore are vulnerable to disturbance. The 2009 population estimate was approximately 387,000 Indiana bats, which is less than half as many as when the species was listed as endangered in 1967 (USFWS, 2007).

When tabulated in 2007, Missouri contained 6 Priority 1 ($\geq 10,000$ bats), 7 Priority 2 ($\geq 1,000$, but $< 10,000$ bats), 18 Priority 3 (50-1,000 bats), and 8 Priority 4 (< 50 bats) hibernacula (USFWS, 2007). The Priority classifications are based on the maximum

population numbers estimated during both historical and recent counts. Population estimates are based primarily on winter survey data collected at known Priority 1 and 2 hibernacula. In 2009, the population estimate for Missouri was approximately 40,000 individuals. However, in 2012 the largest known Indiana bat hibernaculum was discovered in a northeast Missouri county (USFWS, 2013). As such, the 2013 population estimate for Missouri was approximately 140,000 individuals, which is approximately 26% of the range-wide population (USFWS, 2013).

The southern portions of Missouri are more karst in nature with a greater number of caves and larger tracts of forest (Chapman *et al.*, 2002). The northern portions of the state are flatter glaciated plains with more fragmented forest tracts intermingled with a web of crops, pasture, and prairies (Chapman *et al.*, 2002). Indiana bats overwinter in caves and mines in at least 19 Eastern and Midwestern states (USFWS, 2007). Most begin to enter these hibernacula, to which they return each year, by October and November and will remain there until spring emergence. Indiana bats have been found to hibernate in groups up to 5000 bats per square meter (LaVal and LaVal, 1980; Clawson *et al.*, 1980). Missouri hibernacula occur more in the central, southern, and southeastern portions of the state. Of the 269 maternity colonies that were known in 16 states in 2007, Missouri ranked 5th in the US with 20 colonies (USFWS, 2007). These colonies were within 19 counties that range from the north and northeast to the southeast portions of the state.

In the winter of 2006–2007, an emerging disease in bats was documented in a cave in Schoharie County, New York (Blehert *et al.*, 2009). Known as White-nose Syndrome (WNS), the disease is caused by a fungus known as *Pseudogymnoascus*

destructans (Warnecke *et al.*, 2012), which grows on the dermis of bats and disrupts physiology and interrupts hibernation leading to overwinter mortality (Reichard and Kunz, 2009; Brownlee-Bouboulis and Reeder, 2013). By 2012, WNS was estimated to have killed more than 5.7 million bats in North America (USFWS, 2012) and 100% mortality has been observed of some species in some hibernacula (USFWS, 2012). WNS mainly effects cave hibernating bats during the winter. Little brown bats (*Myotis lucifugus*), northern long-eared bats (*Myotis septentrionalis*), tri-colored bats (*Perimyotis subflavus*) and Indiana bats are significantly affected by WNS. Big brown bats (*Eptesicus fuscus*) and Virginia big-eared bats (*Corynorhinus townsendii virginianus*) share caves with these species but are affected far less. Species such as the eastern red bat (*Lasiurus borealis*), evening bat (*Nycticeius humeralis*), and silver-haired bat (*Lasionycteris noctivagans*) are unaffected by WNS because they do not hibernate in caves. The presence of the fungus has been detected on these bats but there has been no mortality associated with those findings.

Indiana bats begin to emerge from their hibernation sites by April or May, but timing can vary depending on latitude and weather (Hall, 1962). Many studies indicate that females tend to emerge from hibernation before males (USFWS, 2007). During spring staging, males typically remain near their hibernacula, within 4-16 kilometers (Rommé *et al.*, 2002), whereas females begin migrating up to hundreds of kilometers to their summer maternity habitats. In Michigan, Winhold and Kurta (2006) documented twelve female bats traveled an average of 476 kilometers between their summer and winter habitats, with a maximum migration distance of 574 kilometers.

Reproductive females form maternity colonies in late spring/early summer, during which time they give birth and rear their young. They give birth to one pup each summer with an approximate 60-day gestation period, and young become volant at around 4 weeks of age. Maternity colonies typically contain 100 or fewer adult females, although some studies have reported more (USFWS, 2007). As many as 384 bats were observed exiting one roost in Indiana (Whitaker and Brack, 2002). Females that form maternity colonies during summer do not necessarily hibernate in the same caves (Boyles *et al.*, 2009). However, females do show strong fidelity to their summering habitats and to their hibernacula (Humphrey *et al.*, 1977; Callahan *et al.*, 1997).

In the fall, Indiana bats migrate to their winter habitats and take part in an activity known as “swarming”, in which bats fly in and out of hibernacula entrances from dusk to dawn (Cope and Humphrey, 1977). This activity takes place for several weeks and mating occurs during this time. In addition, it is thought that individuals are also feeding intensely to build fat reserves in preparation for hibernation (Hall, 1962). Adult females have delayed fertilization, storing sperm through the hibernation period and undergoing fertilization in the spring time (Guthrie, 1933).

Maternity colonies may utilize multiple roost trees. The key characteristic necessary for a tree to be used as a maternity roost is the presence of exfoliating bark or crevices in the tree (Callahan, 1993). These cracks, crevices, and voids provide cover for the bats while allowing for solar exposure. Roost trees with higher sun exposure allow for greater growth rates of the pups, as prenatal and postnatal growth are controlled by the rate of metabolism and body temperature; therefore, warm roost temperature is considered a favorable characteristic for roost tree selection (Racey, 1982). Dead or

dying trees of multiple species have been found to be used as Indiana bat maternity roost trees, including hickories (*Carya spp.*), white oaks (*Quercus alba*), silver maples (*Acer saccharinum*), and American elms (*Ulmus americana*) (USFWS, 2007). Live trees, such as shagbark hickory (*Carya ovata*) and other hickory species that have bark capable of housing bats, have also been identified as Indiana bat maternity roosts (USFWS, 2007). Both dead and live roost trees tend to be larger in size than other trees in the area (Hayes, 2003; USFWS, 2007).

Indiana bats switch maternity roosts on average every 2-3 days (Kurta, 2005). In Missouri, maternity colonies have been shown to use 10-20 roost trees within one summer (Miller *et al.*, 2002). Generally, roosts are separated into two categories, primary and alternate roosts. Callahan (1993) defined “primary” roost trees as those having more than 30 bats during at least two separate exit counts. During an exit count, a researcher watches the roost tree at dusk and counts the bats exiting the roost. “Alternate” roost trees are those used by smaller numbers of bats (Callahan, 1993). However, this distinction may not be suitable for smaller colonies (Kurta *et al.*, 1996) and could include roosts that have had at least one Indiana bat roosting in them at one time. In the face of WNS and increased anthropogenic encroachment, colonies could be reduced in number and size.

Maternity roost habitat could be described in two ways, micro and macrohabitat. Microhabitat variables are a measure within one roost tree such as tree species, the percentage of sloughing bark on the tree, or how much solar exposure the tree receives. These parameters describe what bats would desire in a particular tree to be a maternity roost. Conversely, macrohabitat variables are a measures that contain entities larger than

one tree such as local elevation, distance to some feature, or water resource availability in the area. These parameters describe what particular area bats would select in which to search for a maternity roost tree. Many studies have been conducted to evaluate microhabitat of Indiana bat maternity roost trees (Humphrey *et al.*, 1997; Gardner *et al.*, 1991; Kurta, 2005; Timpone *et al.*, 2010). The macrohabitat features that Indiana bats use to select roost trees are less understood. Studies have been conducted that evaluate or describe landscape scale variables of maternity roost trees in the northeastern portion of the United States (Weber and Sparks, 2013; Watrous *et al.*, 2006), but little has been done in the Midwest. However, Yates and Muzika (2006) did investigate bat activity at various landscape scales in Missouri using echolocation calls to document presence. Macro-habitat selection is a dynamic process that needs more research to better aid in developing management tools that will successfully conserve and contribute to the recovery of Indiana bats.

MaxEnt

MaxEnt is a program for modelling species distributions from presence-only species records (Elith *et al.*, 2011; Phillips *et al.*, 2004). A number of new approaches (e.g., BIOCLIM, DOMAIN, GARP, MaxEnt) have been developed that utilize only presence locations, thereby eliminating the need for true absence locations (Baldwin, 2009). This approach estimates the most uniform distribution (maximum entropy) of sampling points compared to background locations given the constraints derived from the data (Baldwin, 2009). These background locations provide MaxEnt with a range of values for your chosen environmental variables across the study area. MaxEnt uses the

principle of maximum entropy to optimize the coefficients in a generalized linear regression providing a method that is well suited for species distribution modeling (Phillips *et al.*, 2006). The ‘presence only’ case is an interesting one. Generally, presence-absence data are evaluated by comparing variables associated with areas of presence to variables associated with areas of probable absence. The data set evaluated in this study is inherently presence only (*i.e.*, I did not evaluate random trees to identify those that were confirmed to not be Indiana bat maternity roost trees).

MaxEnt’s predictive performance is consistently competitive with the highest performing species distribution modeling methods (Elith *et al.*, 2011). The outputs of MaxEnt include a raster GIS file and, if selected, variable response curves, pictures of the predictions, and results of a jackknife test for importance of variables. In addition, an area under the curve (AUC) value is provided for the model. This value is a measure of the accuracy of the model based on the training data’s ability to predict the test data. An AUC value of 0.5 is the same as a random choice. An AUC value of 1.0 would represent a perfect model and is not functionally attainable.

Model Selection

Recent studies have demonstrated a need for increased rigor in building and evaluating ecological niche models (ENMs) based on presence-only data (Muscarella *et al.*, 2014). MaxEnt currently has six feature classes, or mathematical relationships: linear, product, quadratic, hinge, threshold and categorical (Elith *et al.*, 2011). The choice of which features are used defines the statistical manner by which MaxEnt evaluates the environmental data, and as such, variation of feature choice leads to

variation in model performance. The software ENMTools has been developed with tools that can help the user to determine model performance (Warren *et al.* 2008; Warren and Seifert, 2011). This enables a straightforward way to quickly evaluate the Akaike Information Criterion (AIC) values of several MaxEnt models. AIC is a metric evaluating the quality of a statistical model provided a given dataset, with respect to model complexity. Or to say, within a group of models that use a shared dataset, AIC estimates the quality of each model relative to the other models in the group. In addition, ENMTools provides the AICc metric, which is an AIC with a correction calculation which helps eliminate over fitting when sample size is small. The resultant values produced from the AIC and AICc processes vary based on the structure of the models evaluated. The comparison of these values is relevant among models of the same structure. Therefore, AIC and AICc values from this study may not be comparable to those in other studies.

Study Objectives

This study will evaluate macrohabitat, or landscape scale variables associated with the location of known Indiana bat roost trees across six counties in north central Missouri (Fig. 1). I will determine which feature type/s best fit the structure of my dataset within the MaxEnt modeling program. Once the preferred model is identified, I will evaluate which landscape scale variables contribute most to the model. Finally, predictive maps will be produced identifying where in the 6 county area have the highest probability of the occurrence of Indiana bat maternity roost habitat.

METHODS

Field Methods

During 2008–2011, between 15 May and 15 August, mist-netting was performed across six counties in northern Missouri with the goal to capture reproductive (*i.e.*, pregnant, lactating, or post-lactating) adult female Indiana bats and their young of the year. These data would confirm the presence of a maternity colony in the area. Various sized (4, 6, 9, and 12 m), low visibility mesh mist nets were placed in potential travel corridors within known or suspected maternity roosting areas. Both single tier net setups and stacked tier setups were utilized. The latter utilize multiple mist nets overlapped vertically to gain additional height. Surveys were conducted beginning at sunset and were continued for at least 5 hours, depending on bat activity levels and weather. Nets were checked at least every 10 minutes to minimize stress to any captured bats. Additionally, the U.S. Fish and Wildlife Service (USFWS) Range-wide Indiana Bat Summer Survey Guidelines (2007) and U.S. Geological survey (USGS) WNS decontamination procedures were followed. Collection techniques were authorized under Missouri State University's Institutional Animal Care and Use Committee (IACUC) protocol 2008N (March 23rd, 2009), Federal Fish and Wildlife Collectors Permit # TE02365A-1, and Missouri Wildlife Collector's Permit # 14817.

Captured reproductively active female Indiana bats were fitted between the scapulas with a 0.29 g radio transmitter (Holohil systems Ltd., Ontario, Canada) utilizing Skin-Bond surgical adhesive. Once the glue was dry bats were released at the capture location. Bats were not held for more than 20 minutes. Bats were tracked using 3 and 5 element Yagi antennas with a 148-152MHZ telemetry receiver (Communication

Specialists, Inc., Orange, California). Each bat was tracked for the life of the transmitter. Lost signals were attempted to be found for two weeks after the loss of the signal.

Many bats were radio-tracked to multiple roost trees. Each roost in which a transmitter was present was observed for a minimum of two separate evenings at sunset to count roost occupants. Roost trees were categorized based upon the number of bats observed exiting the tree during an exit count following Callahan's (1993) roost classification system. In addition, I propose a third designation: roost trees that were visited multiple times by multiple bats but did not contain >30 individuals were designated as "secondary" roosts. I only used primary and secondary roost trees in these analyses. The omission of alternate roosts that do not meet the definition of secondary eliminates trees that only a single bat visited. This was done after observing that bats often visit a tree the first night after being fitted with a radio tag and are not observed visiting that tree again. No roosts trees that had multiple bats for only one night were found during this study. Once a roost was confirmed to be either primary or secondary, its location was recorded with a PN-60 GPS device (Delorme, Yarmouth, Maine) with an accuracy of < 5 m.

Analyses

Primary and secondary roost tree locations were compiled into a single shapefile in ArcGIS 10.1 (ESRI, Redlands, California). Locations of each roost tree were projected into Universal Transverse Mercator (UTM) zone 15N, for analysis. This projection was chosen to align with the default projections of the landscape variables acquired for the study.

Landscape scale variables were chosen based on GIS data that was available in 30M or smaller resolution. All variables were compiled into raster format with the same cell size and geographic extent in ArcGIS 10.1. Specifically, the Snap Raster setting within the tool environments workspace was used for ensuring exact spatial extent for all the landscape variables. All environmental variables are continuous data, have a 30m spatial resolution, and were created within the last 20 years. The digital elevation model (DEM) and stream network files were acquired from the Missouri Spatial Data Information Service, (<http://msdis.missouri.edu/>). Slope and aspect files were derived from the DEM via the Spatial Analyst extension for ArcGIS 10.1. The distance to stream variable was created by populating a blank raster with data calculated from the vector stream file utilizing the ArcGIS tool Euclidian Distance. The land cover type, specifically known as the National Land Cover Dataset (NLCD), and forest canopy files were acquired from the Multi-Resolution Land Characteristics Consortium (MLRC), (<http://www.mrlc.gov/>). Forest canopy is a raster file containing the percentage of canopy value for each 30 meter cell. The distance to forest edge variable was created by populating a blank raster with the data calculated from the categorical raster NLCD utilizing the ArcGIS tool Euclidian Distance; all forest land use types were used.

The Indiana bat roost tree data utilized in this study are inherently “presence only.” In addition, I am not modeling a certain tree species. Rather, I am modeling a location of a tree that bats choose to use as a roost. Not only are these roosts an ephemeral resource, but they can be one of several different species and of different levels of decay.

I utilized MaxEnt, version 3.3.3k, to model the probability of occurrence based on 20 confirmed primary and secondary Indiana bat roost trees within a six county area in northern Missouri (Phillips *et al.*, 2006). Primary and secondary roosts trees were lumped for analyses. I randomly selected 75% of the roost locations, through a random number generator in Microsoft Excel, to train the model and the remaining 25% to test the model (Fig. 2). These same random sets were used for each of the model selection runs. I chose the ‘raw’ data output as the best option for estimating probability of occurrence (Yackulic, 2013).

I ran MaxEnt 10 times utilizing a different set of feature types for each run (Table 2). I utilized ENMTools version 1.4.4 to evaluate which of these 10 feature type models had the lowest AICc value/s. MaxEnt was run again using the feature type/s identified in the previous 10 model series as the preferred model/s. I used the replicate option with cross-validation allowing the model to run with four iterations. As such, each point in the dataset was used for training three times and once for testing.

Response curves were created to show how predicted relative probability of occurrence depends on the value of each environmental variable. Also, I used a jackknife approach to evaluate the importance of each variable. In this, each variable is excluded in turn and a model estimated with the remaining variables; then a model is estimated using each variable in isolation (Phillips, 2006).

MaxEnt keeps track of how each variable contributed to making the model. The “percent contribution” value represents model gain increase for each environmental variable while training the model. At the end of the training process these values are converted to percentages. The “permutation importance” value that is calculated refers to

variable contribution of the final MaxEnt model. This provides a more realistic explanation of how each variable contributed to the model.

RESULTS

Through compilation of data from multiple Indian bat survey projects, 20 primary and secondary Indiana bat maternity roost trees were identified. The roost status of these trees was confirmed with a minimum of two nightly roost counts for each tree.

Ten separate MaxEnt models were created utilizing a variety of feature type combinations. The model created using the linear feature had the lowest AICc and the model created using the quadratic feature had the next lowest AICc (Table 1). No other model was within two AICc units of the preferred model. Therefore, only linear and quadratic were considered equally supported as the preferred models, and used in subsequent analysis to evaluate the importance of each variable. The models that were created with the 'hinge' feature yielded no AICc values because they had too many parameters for the number of data points available.

Two separate MaxEnt models were then created using the linear and quadratic features with 4 replicates each, and the cross-validation option to evaluate environmental variable contribution (Figs 3 & 4). The AUC value (mean + SD) for the linear model was $0.792 + 0.056$ and for the quadratic model was $0.764 + 0.056$.

Response curves reflect the dependence of predicted suitability on the value gradients for each variable. Generally speaking, roosts tended to be in areas of larger amounts of forest canopy, closer to the forest edge, at higher elevation, with a greater slope, and closer to streams (Figs. 5-16).

Some variables contributed more than others to the linear and quadratic MaxEnt model (Tables 2 & 3). In both models, the distance (closer) to forest edge variable

provided the highest permutation importance followed by elevation (higher) and distance (closer) to stream. The slope and percent forest canopy varied in their permutation importance among the models. The aspect variable provided zero percent contribution and permutation importance in both models.

Different than the contributions presented above, the jackknife test using AUC on test data shows how each variable affects the prediction when withheld from the model and when used in isolation (Figs 17 & 18). The variable that decreases the linear model performance the most when omitted is elevation. This indicates that elevation has the most predictive information that isn't provided by the other variables. However, the percent forest canopy variable provides the most predictive information when used in isolation. In the quadratic model, the distance to forest edge variable decreases the model performance the most when omitted, followed closely by elevation. Interestingly, the slope variable provides the most predictive information when used in isolation. In both models, the aspect variable decreases predictive value of the model dramatically when used in isolation.

A predictive map was produced for each model (Figs. 19 & 20). With the color scheme set to the same occurrence probabilities in each map the linear model predicts more high probability areas, shown in white, than the quadratic model.

DISCUSSION

Combining the information from the response curves, variable contribution tables, and the jackknife tables yields the best understanding of which variables play the largest role in predicting the probability that an Indiana bat roost tree will be found in a given location within the study area.

It makes sense for the most influential variable in the model to be distance (closer) to forest edge. The availability of trees with high solar exposure is high near the forest edge. The fact that these areas are also close to streams further strengthens the predictions of the model. So, within a fairly close area the bats could have a water source, plenty of forest edge for foraging, and a large selection of trees with varying degrees of solar exposure.

The model indicates that roost trees are closer to streams and at higher elevations. This is an apparently contradictory result. Generally, one would expect areas closer to streams to be in the lower elevations. This can be explained by the topography of the area. The six counties in my study area are highly agricultural but interspersed with fingers of forested areas. These forest fingers tend to be around the low lying stream areas with trees extending up to where the elevation plateaus and the trees have been cleared for agriculture. Both models show that the roost trees are located closer to the forest edge. Therefore, the forest edges can be located at relatively high elevations. At the same time these locations are also near the streams.

Interestingly, the slope variable had a high level of predictive value in the jackknife test when used in isolation but actually increased the overall predictability of

both models when omitted. This indicates that slope could be a correlated variable. The slope value range for the roost locations was relatively low, 0-12 degrees, with 6-7 degrees being the mean. Within the study area, the locations with the steepest slope also tends to be near the forested riverine fingers.

These predictive models may only be relevant in areas of the Midwest U.S. where there are similar habitat variables and in areas where Indiana bats are known to occur. However, this same technique could be used in other areas to better understand what landscape variables play a role in roost tree habitat selection.

Management Implications

With the proliferation of wind energy projects, transmission line construction, and other anthropogenic expansion, the locational identification and spatial quantification of Indiana bat maternity roost habitat is becoming more important. The proponents of these projects are required to determine their level of impact on endangered species for permitting and mitigation purposes. My research helps to provide a repeatable process by which project proponents can furnish these data to the relevant regulatory agencies. In addition, during USFWS required Indiana bat surveys, surveyors are required to track Indiana bats to their roost trees. My research can be used to help identify maternity roost habitat suitability within or adjacent to proposed project areas. In addition, this process can be used to identify areas for future mitigation areas. These predictions also provide a strategy for deploying acoustic detectors. For identifying roost trees, micro-habitat factors should be used in conjunction with this method.

Future Work

The program MaxEnt provides a means to model potential species distribution with presence-only data. This process could be used to evaluate foraging habitat of Indiana bats or a number of other important ecological questions for a variety of protected species. Also, other potentially important landscape variables; such as distance to roadway, distance to populated areas, or percent forest edge, could be added to the model depending on ecological factors in different areas. These additions could bolster the model and improve predictability. However, the addition of variables has the potential to increase the problem of correlation between or among variables and would require more presence points.

REFERENCES

- BALDWIN, R. 2009. Use of Maximum Entropy Modeling in Wildlife Research. *Entropy*, **11**:854-866.
- BARBOUR, R. W. AND W. H. DAVIS. 1969. Bats of America. University Press of Kentucky, Lexington. 286 p.
- BLEHERT, D. S., A. C. HICKS, M. BEHR, C. U. METEYER, B. M. BERLOWSKI ZIER, E. L. BUCKLES, J. T. H. COLEMAN, S. R. DARLING, A. GARGAS, R. NIVER, J. C. OKONIEWSKI, R. J. RUDD, AND W. B. STONE. 2009. Bat white-nose syndrome: an emerging fungal pathogen? *Science*, **323(5911)**:227-227.
- BOYLES, J., J. TIMPONE, AND L. W. ROBBINS. 2009. Bats of Missouri. ISU Center for North American Bat Research and Conservation. 60 p.
- BROWNLEE-BOUBOULIS, S. A., AND D. M. REEDER. 2013. White-nose syndrome-affected little brown Myotis (*Myotis lucifugus*) increase grooming and other active behaviors during arousals from hibernation. *Journal of Wildlife Distribution*, **49**:850-859.
- CALLAHAN, E. V. 1993. Indiana Bat Summer Habitat Requirements. M.S. Thesis. University of Missouri, Columbia. 84 p.
- CALLAHAN, E. V., R. D. DROBNEY, AND R. L. CLAWSON. 1997. Selection of summery roosting sites by Indiana bats (*Myotis sodalis*) in Missouri. *Journal of Mammalogy*, **78**:818-825.
- CHAPMAN, S. S., J. M. OMERNIK, G. E. GRIFFITH, W.A. SCHROEDER, T. A. NIGH, AND T. F. WILTON. 2002. Ecoregions of Iowa and Missouri (color poster with map, descriptive text, summary tables, and photographs). Reston, VA. U.S. Geological Survey (map scale 1:1,800,000).
- CLAWSON, R. L., R. K. LAVAL, M. L. LAVAL, AND W. CAIRE. 1980. Clustering behavior of hibernating *Myotis sodalis* in Missouri. *Journal of Mammalogy*, **61**:245-253.
- COPE, J. B. AND S. R. HUMPHREY. 1977. Spring and autumn swarming behavior in the Indiana Bat, *Myotis sodalis*. *Journal of Mammalogy*, **58**:93-95.
- ELITH, J., S. PHILLIPS, T. HASTIE, M. DUDIK, Y. CHEE, AND C. YATES. 2011. A Statistical Explanation of MaxEnt for Ecologists. *Diversity and Distributions*, **17(1)**:43-57.

- GARDNER, J. E., J. D. GARNER, AND J. E. HOFMANN. 1991. Summary of *Myotis sodalis* summer habitat studies in Illinois: with recommendations for impact assessment. Report prepared for Indiana/Gray bat Recovery Team Meeting, Columbia, MO 28 p.
- GUTHRIE, M. J. 1933. The reproductive cycle of some cave bats. *Journal of Mammalogy*, **14**:199-216.
- HALL, J. S. 1962. A life history and taxonomic study of the Indiana bat, *Myotis sodalis*. Reading Public Museum and Art Gallery, *Scientific Publications*, **12**:1-68.
- HAYES, J. P. 2003. Habitat ecology and conservation of bats in western coniferous forests. p. 81-199 *In*: C. J. Zabel and R. G. Anthony (eds.). Mammal community dynamics in coniferous forests of western North America: management and conservation.
- HUMPHREY, S. R., A. R. RICHTER, AND J. B. COPE. 1977. Summer habitat and ecology of the endangered Indiana bat, *Myotis sodalis*. *Journal of Mammalogy*, **58**:334-346.
- KURTA, A. 2005. Roosting ecology and behavior of Indiana bats (*Myotis sodalis*) in summer. p.29-42. *In*: K.C. Vories and A. Harrington (eds.). Proceedings of the Indiana bat and coal mining: a technical interactive forum. Office of Surface Mining, U.S. Department of the Interior, Alton, IL.
- KURTA, A., K. J. WILLIAMS, AND R. MIES. 1996. Ecological, behavioral, and thermal observations of a peripheral population of Indiana Bats (*Myotis sodalis*). p. 102-117. *In*: R. M. R. Barclay and R. M. Brigham (eds.). Bats and Forests Symposium. Research Branch, British Columbia Ministry of Forests. Victoria, BC, Canada.
- LAVAL, R. K. AND M. L. LAVAL. 1980. Ecological studies and management of Missouri bats, with emphasis on cave-dwelling species. Missouri Department of Conservation. *Terrestrial Series*, **8**:1-52.
- MILLER, N. E., R. D. DROBNEY, R. L. CLAWSON, AND E. V. CALLAHAN. 2002. Summer habitat in northern Missouri. p. 165-171. *In*: A. Kurta and J. Kennedy (eds.). The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, TX.
- MISSOURI SPATIAL DATA INFORMATION SERVICE (MSDIS), University of Missouri. January 22nd, 2015. (<http://msdis.missouri.edu/>)
- MULTI-RESOLUTION LAND CHARACTERISTICS CONSORTIUM (USGS, MLRC). January 22nd, 2015. (<http://www.mrlc.gov/>)

- MUSCARELLA, R., P. J. Galante, M. Soley-Guardia, R. A. Boria, J. M. Kass, M. Uriarte, & R. P. Anderson, 2014. ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution*, **5**(11):1198-1205.
- PHILLIPS, S. 2006. A brief tutorial on Maxent. AT & T Research. Available at: <http://www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc>.
- PHILLIPS, S., M. DUDIK, AND R. SCHAPIRE. 2004. A Maximum entropy approach to species distribution modeling. Proceedings of the Twenty-First International Conference on Machine Learning. ACM. 83.
- PHILLIPS, S. J., R. P. ANDERSON, AND R. E. SCHAPIRE. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**:231-259.
- RACEY, P. A. 1982. Ecology of bat reproduction. p. 57-104. *In*: Kunz T.H. Ecology of Bats. Plenum Press. New York, NY. 425 p.
- REICHARD, J. D., AND T. H. KUNZ. 2009. White-nose syndrome inflicts lasting injuries to the wings of little brown bats (*Myotis lucifugus*). *Acta Chiropterol*, **11**:457-464.
- ROMMÉ, R. C., A. B. HENRY, R. A. KING, T. GLUECK, AND K. TYRELL. 2002. Home range near hibernacula in spring and autumn. p. 153-158. *In*: A. Kurta and J. Kennedy (eds.). The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, TX.
- TIMPONE, J., J. BOYLES, K. MURRAY, D. AUBREY, AND L. W. ROBBINS. 2010. Overlap in roosting habits of Indiana bats (*Myotis sodalis*) and northern bats (*Myotis septentrionalis*). *The American Midland Naturalist*, **163**(1):115-123.
- U.S. FISH AND WILDLIFE SERVICE (USFWS). 2007. Indiana bat (*Myotis sodalis*) draft recovery plan: first revision. U.S. Fish and Wildlife Service, Fort Snelling, MN. 258 p.
- U.S. FISH AND WILDLIFE SERVICE (USFWS). 2012. North American bat death toll exceeds 5.5 million from white-nose syndrome. Arlington, VA: USFWS Office of Communications.
- U.S. FISH AND WILDLIFE SERVICE (USFWS). 2013. 2013 Rangewide Population Estimate for the Indiana bat (*Myotis sodalis*) by USFWS Region. Bloomington, Indiana, Ecological Services Field Office.
(<http://www.fws.gov/Midwest/Endangered/mammals/inba/pdf/2013inbaPopEstimate26Aug2013.pdf>)

- WARNECKE, L., J. M. TURNER, T. K. BOLLINGER, J. M. LORCH, V. MISRA, P. M. CRYAN, G. WIBBELT, D. S. BLEHER, AND C. K. WILLIS. 2012. Inoculation of bats with European *Geomyces destructans* supports the novel pathogen hypothesis for the origin of white-nose syndrome. *Proceedings of the National Academy of Sciences*, **109**(18):6999-7003.
- WARREN, D. L., R. E. GLOR, AND M. TURELLI. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*, **62**(2):868-2883.
- WARREN, D. L., & S. N. SEIFORT. 2011. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, **21**(2):335-342.
- WATROUS, K. S., T. M. DONOVAN, R. M. MICKEY, S. R. DARLING, A. C. HICKS, AND S. L. V. OETTINGEN. 2006. Predicting minimum habitat characteristics for the Indiana bat in the Champlain Valley. *Journal of Wildlife Management*, **70**(5):1228-1237.
- WEBER, T. AND D. SPARKS. 2013. Summer habitat identification of an endangered bat, *Myotis sodalis*, across its eastern range of the USA. *Journal of Conservation Planning*, **9**:53-68.
- WHITAKER, J. AND V. BRACK. 2002. Distribution and Summer Ecology in Indiana. p. 48-54. In: A. Kurta and J. Kennedy (eds.). The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin.
- WINHOLD, L. AND A. KURTA. 2006. Aspects of migration by the endangered Indiana bat, *Myotis sodalis*. *Bat Research News*, **47**:1-11.
- YACKULIC, C., R. CHANDLER, E. ZIPKIN, J. A. ROYLE, J. D. NICHOLS, E. H. C. GRANT, AND S. VERAN. 2013. Presence-only modelling using MaxEnt: when can we trust the inferences? *Methods in Ecology and Evolution*, **4**(3):236-243.
- YATES, M. D. AND R. M. MUZIKA. 2006. Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. *Journal of Wildlife Management*, **70**(5):1238-1248.

Table 1. Feature Type Combinations for MaxEnt Model Runs. The “x” represents feature type combinations that had too many parameters for the number of data points available. The linear and quadratic feature types were both considered the preferred models.

Feature Type/s	AICc Value	Δ AICc
Hinge	x	x
Hinge and Linear	x	x
Linear	640.88	0.00
Linear and Quadratic	650.91	10.03
Linear and Threshold	647.05	6.17
Quadratic	642.15	1.27
Quadratic and Hinge	x	x
Quadratic and Threshold	654.34	13.46
Threshold	659.48	18.60
Threshold and Hinge	x	x

Table 2. Estimates of Relative Contributions of the Environmental Variables for the Linear Model. The “percent contribution” value represents model gain increase for each environmental variable while training the model. The “permutation importance” value refers to the variable contribution of the final MaxEnt model.

Environmental Variable	Percent Contribution	Permutation Importance
Distance to Forest Edge	29.8	34.7
Elevation	33.4	29.2
Distance to Stream	14.9	17.1
Percent Tree Canopy	12.1	16.9
Slope	9.7	2.0
Aspect	0.0	0.0

Table 3. Estimates of Relative Contributions of the Environmental Variables for the Quadratic Model. The “percent contribution” value represents model gain increase for each environmental variable while training the model. The “permutation importance” value refers to the variable contribution of the final MaxEnt model.

Environmental Variable	Percent Contribution	Permutation Importance
Distance to Forest Edge	30.3	40.9
Elevation	29.4	27.1
Distance to Stream	17.1	19.3
Slope	22.2	6.4
Percent Tree Canopy	1.0	6.2
Aspect	0.0	0.0

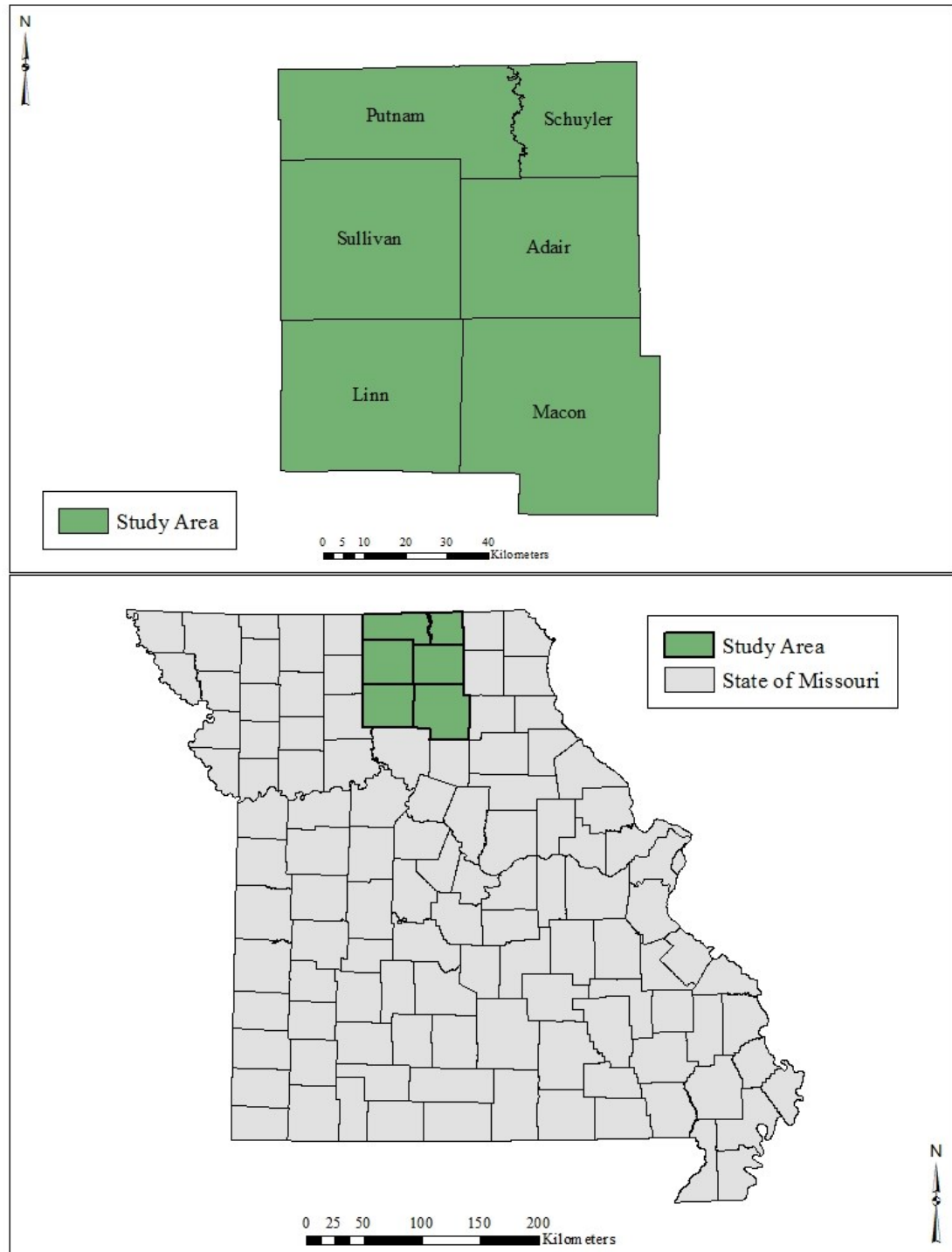


Figure 1. Map Showing Study Area within the State of Missouri.

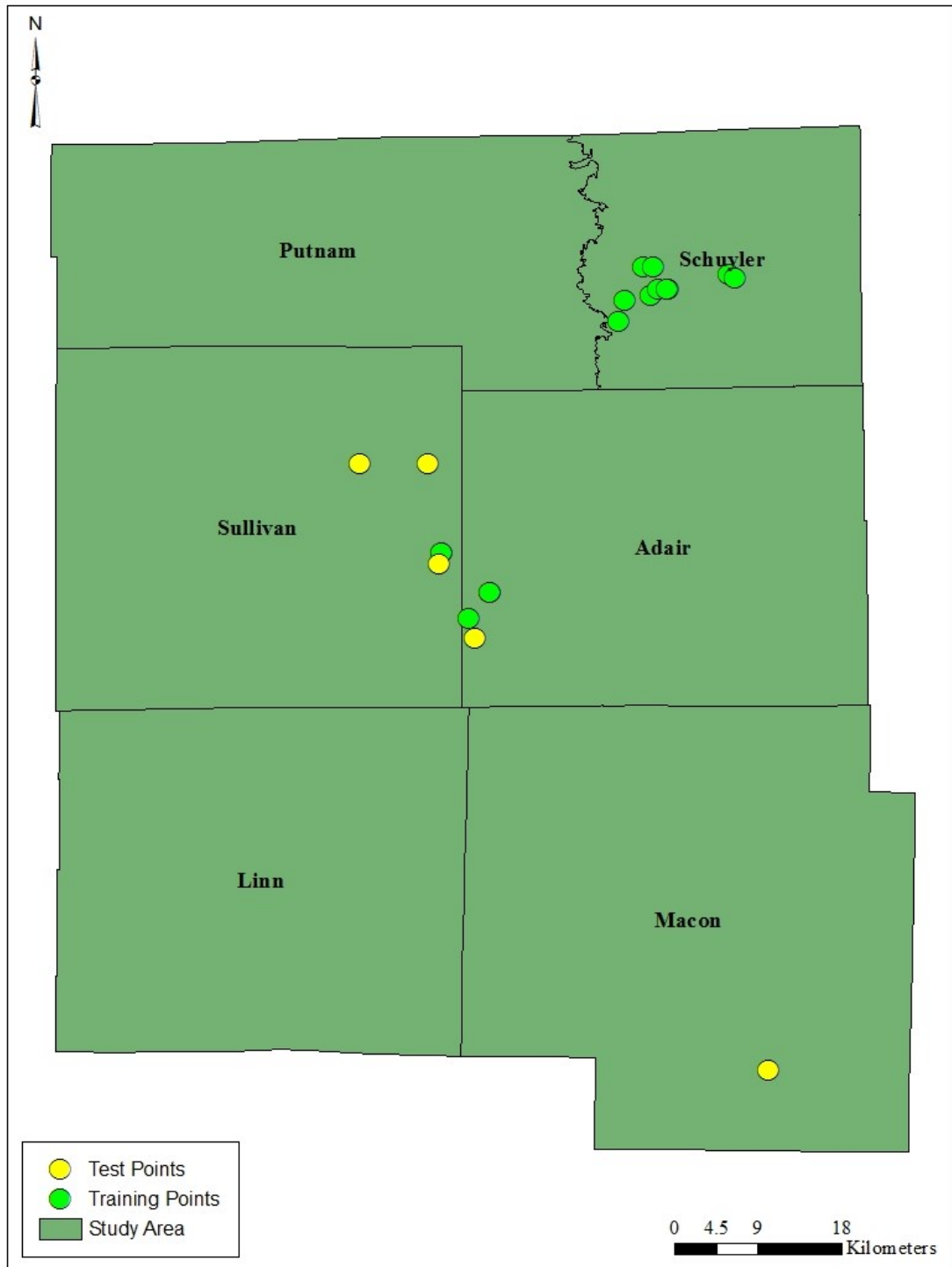


Figure 2. Map Showing location of twenty roost trees within the study area. Fifteen were used to “train the model and 5 were used to then test it.

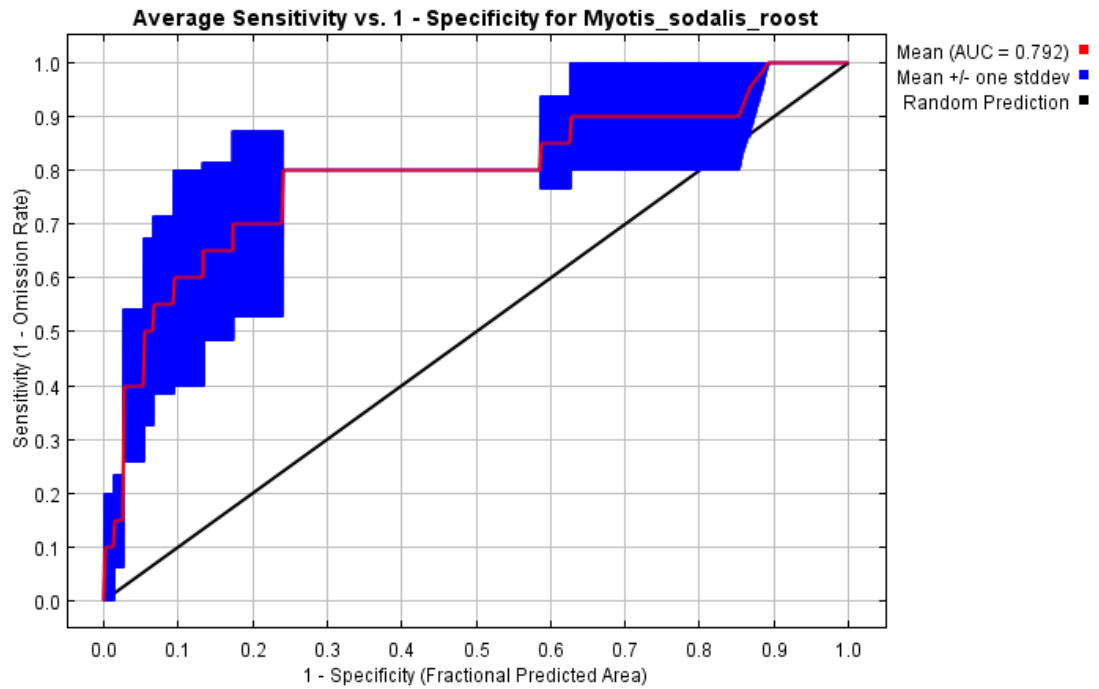


Figure 3. Receiver Operating Characteristic (ROC) Curve (Linear).

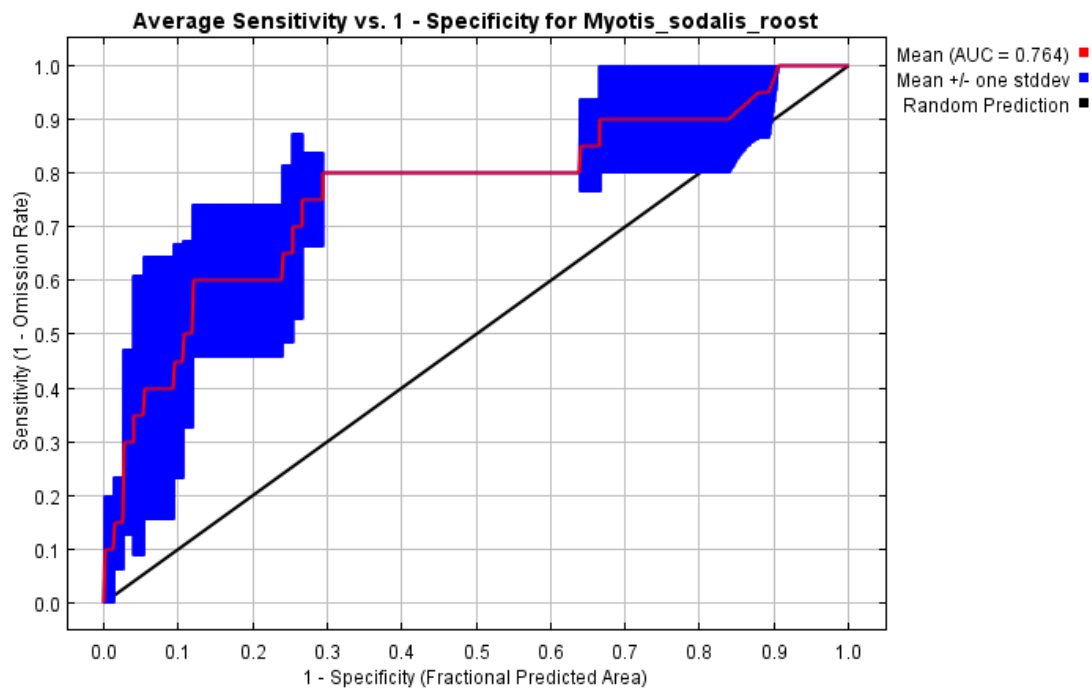


Figure 4. Receiver Operating Characteristic (ROC) Curve (Quadratic).

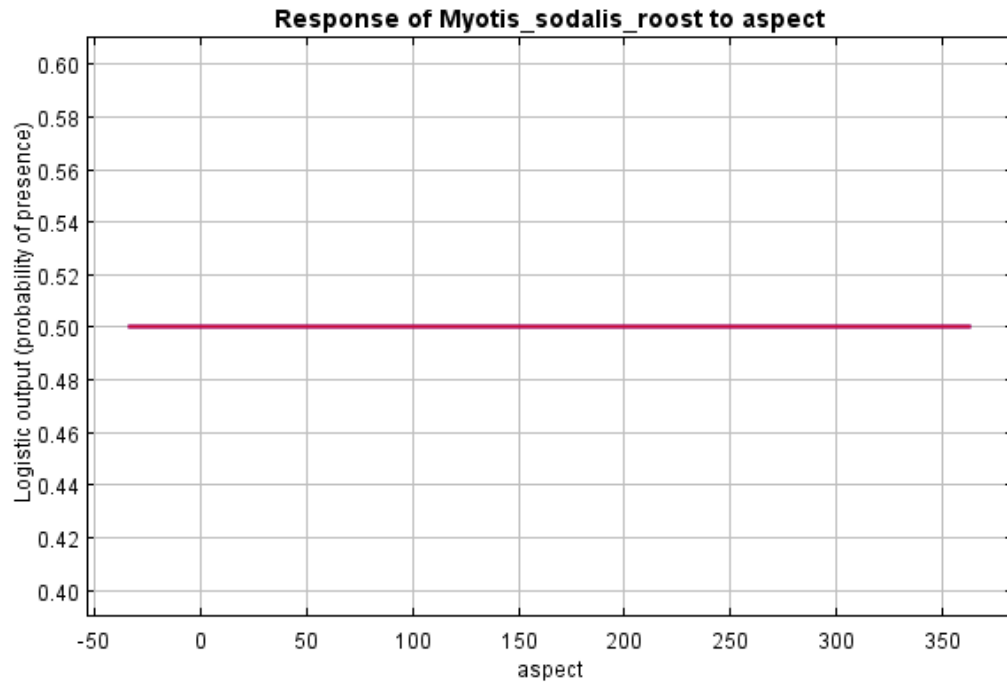


Figure 5. Response Curve for the Aspect Variable (Linear).

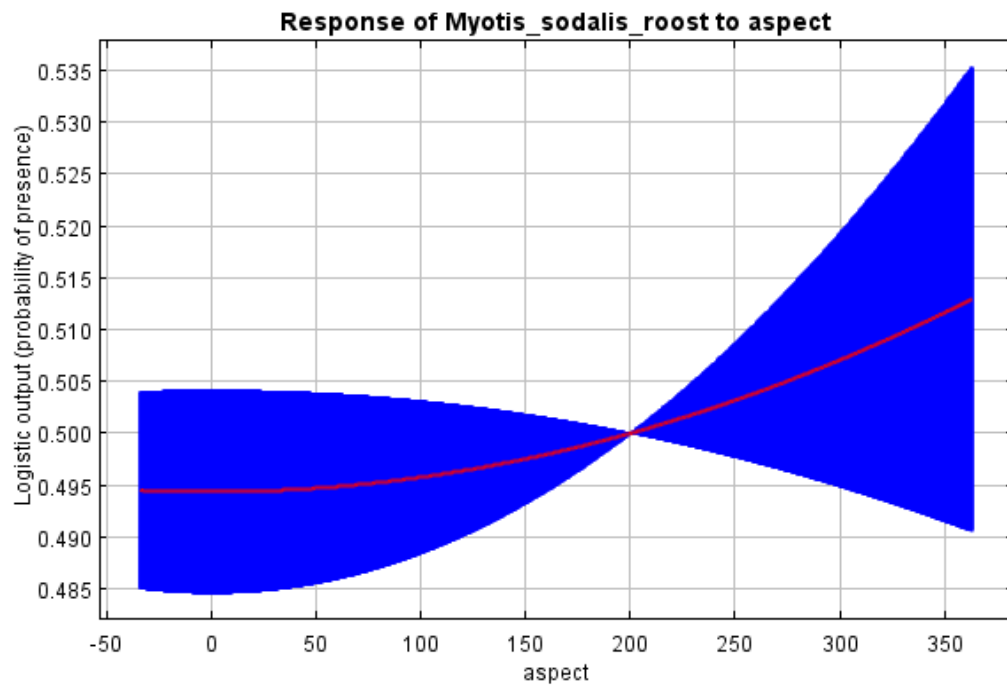


Figure 6. Response Curve for the Aspect Variable (Quadratic).

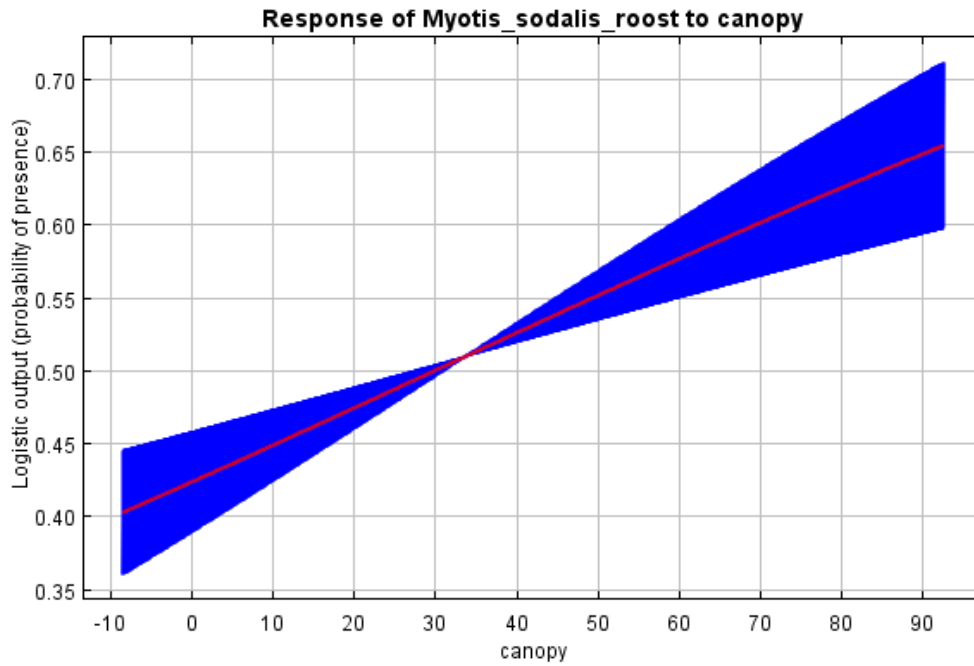


Figure 7. Response Curve for the Percent Forest Canopy Variable (Linear).

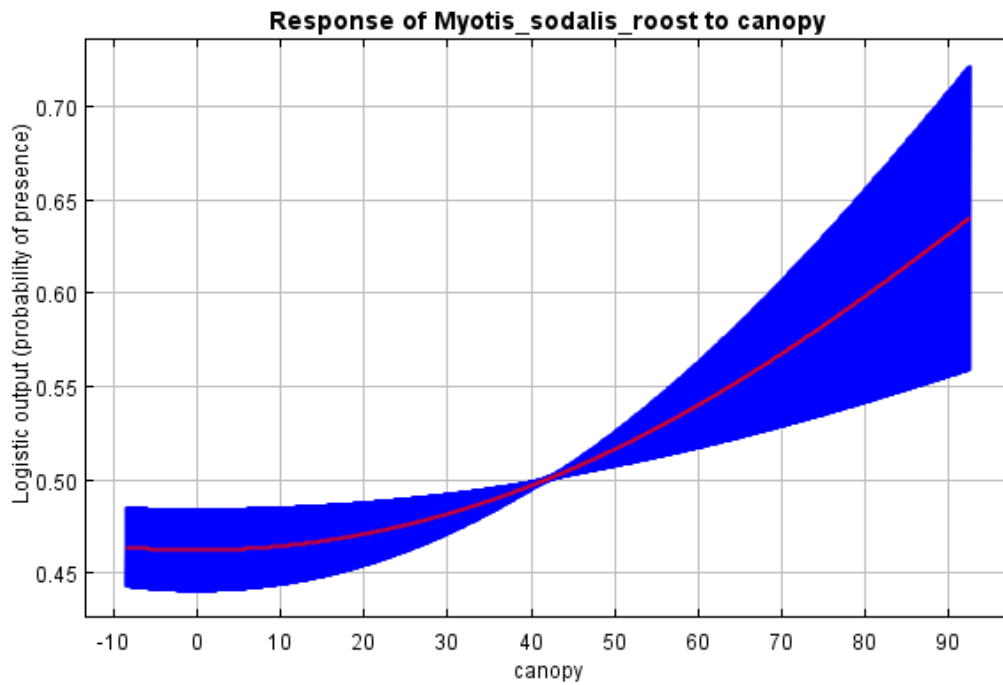


Figure 8. Response Curve for the Percent Forest Canopy Variable (Quadratic).

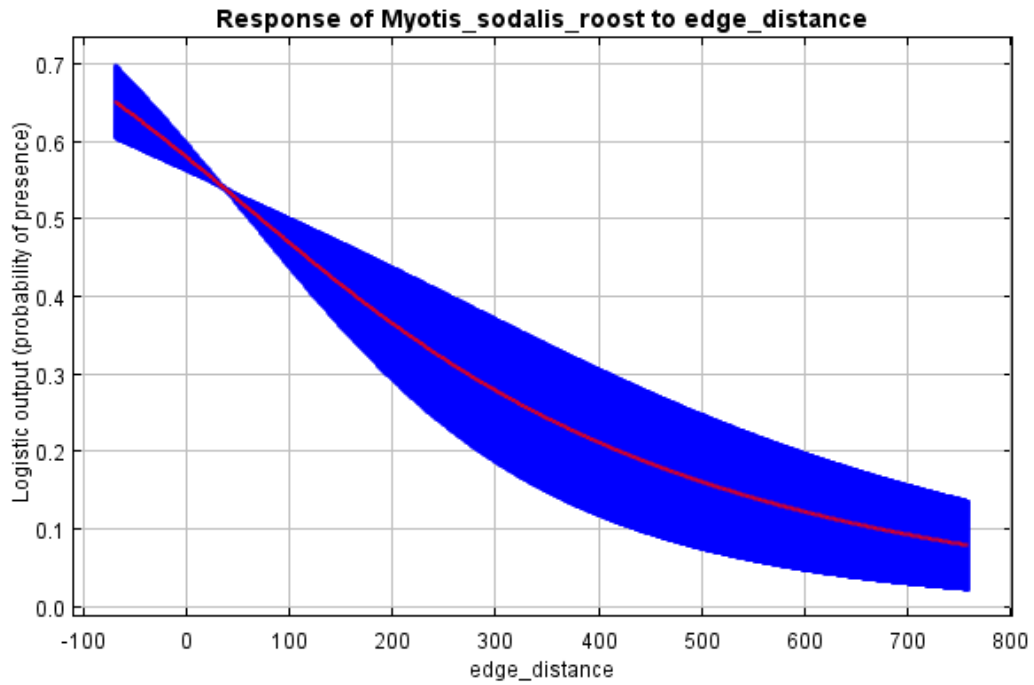


Figure 9. Response Curve for the Distance to Forest Edge Variable (Linear). Distance is calculated in meters.

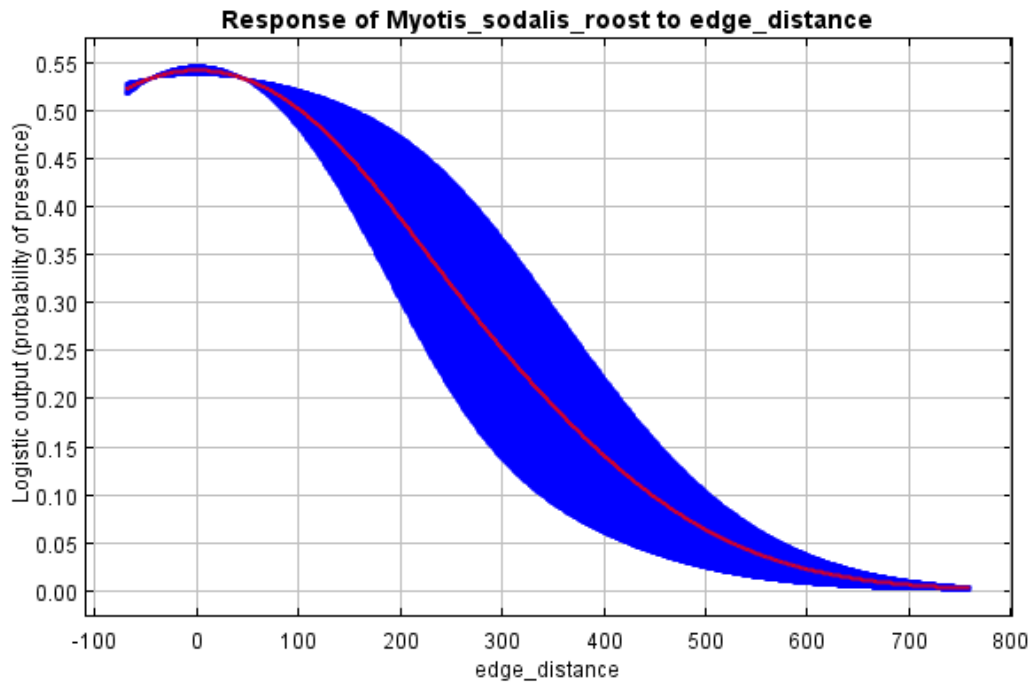


Figure 10. Response Curve for the Distance to Forest Edge Variable (Quadratic). Distance is calculated in meters.

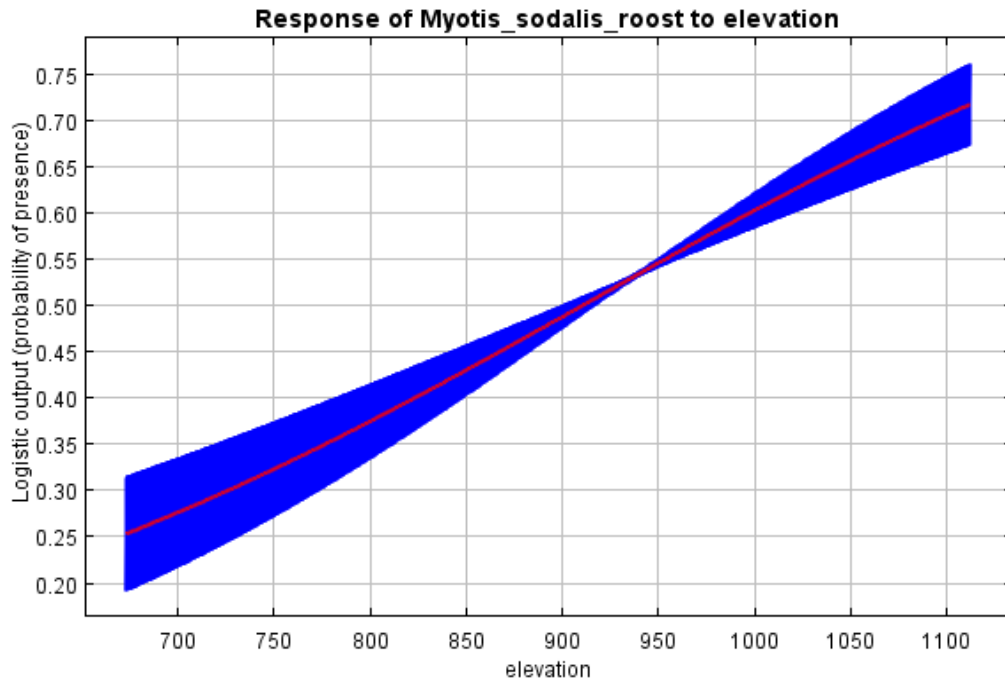


Figure 11. Response Curve for the Elevation Variable (Linear). Elevation is calculated in feet.

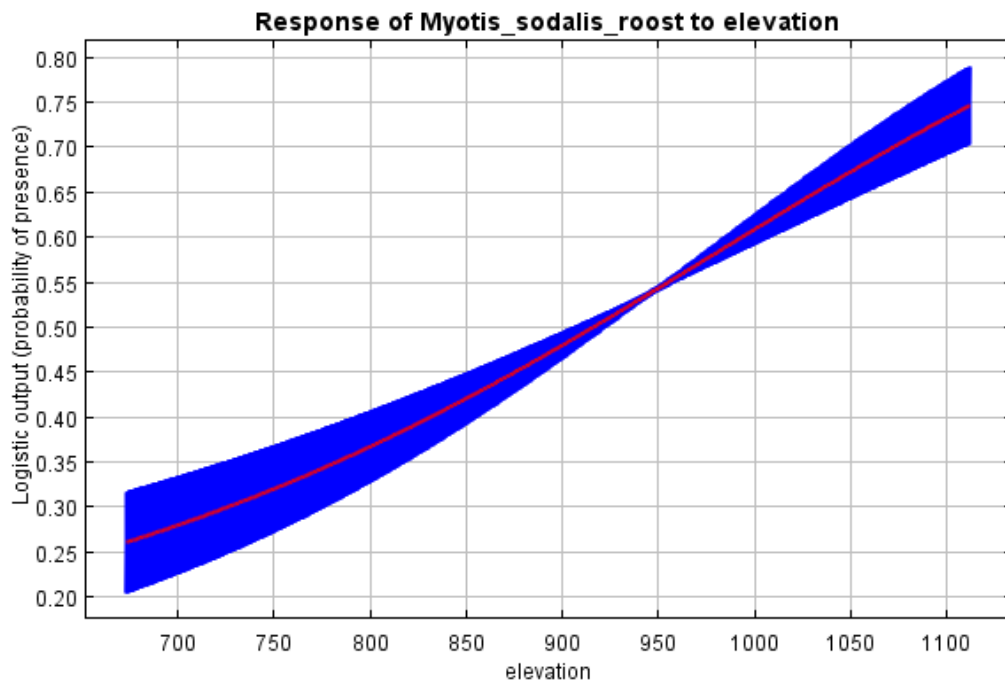


Figure 12. Response Curve for the Elevation Variable (Quadratic). Elevation is calculated in feet.

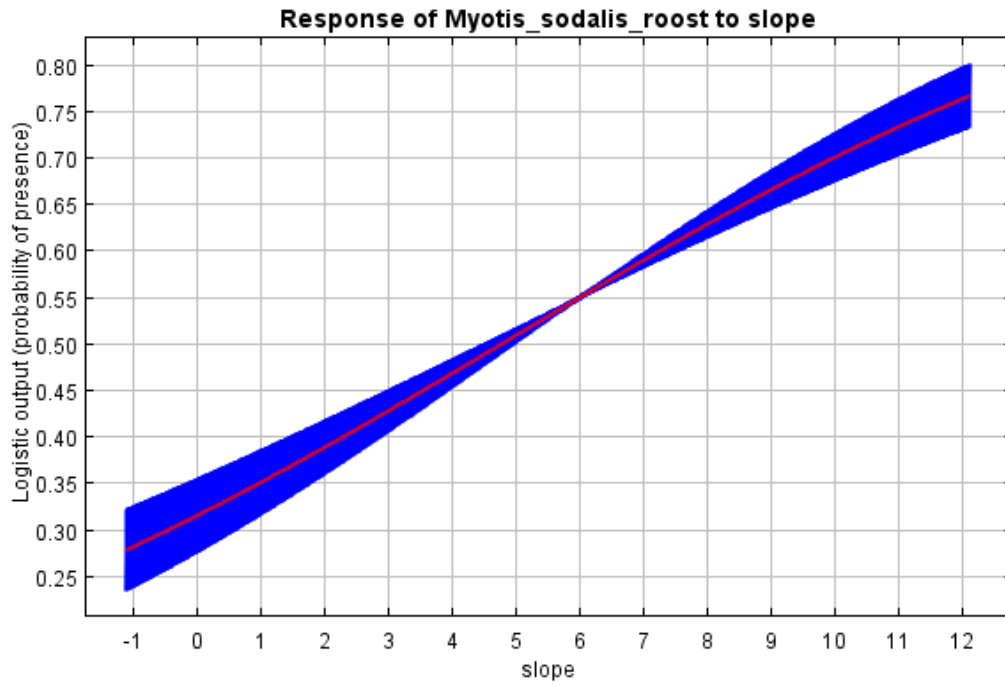


Figure 13. Response Curve for the Slope Variable (Linear).

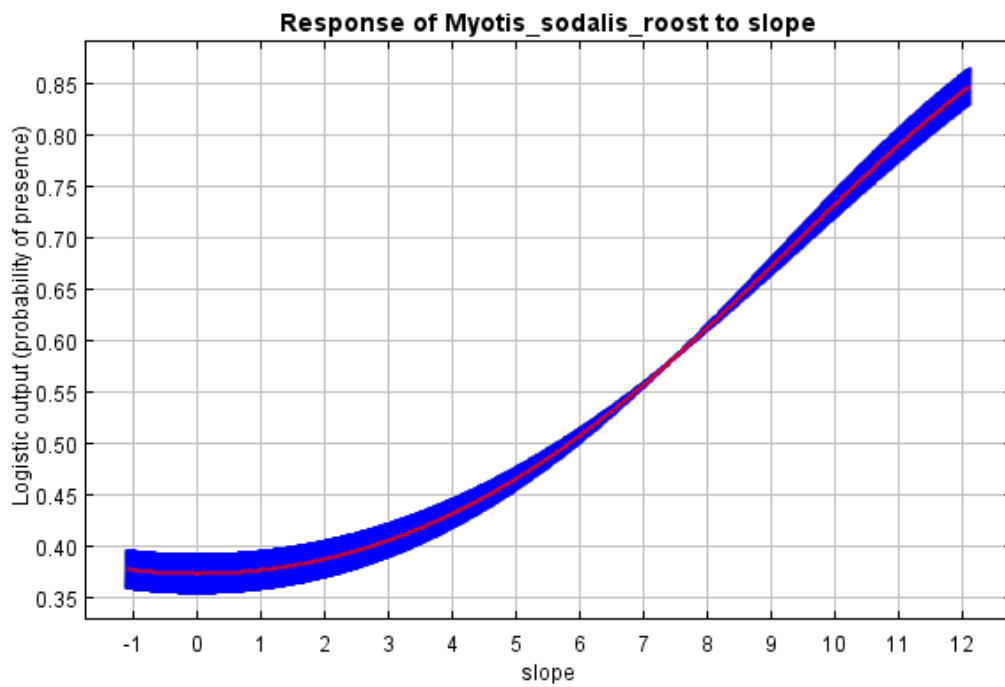


Figure 14. Response Curve for the Slope Variable (Quadratic)

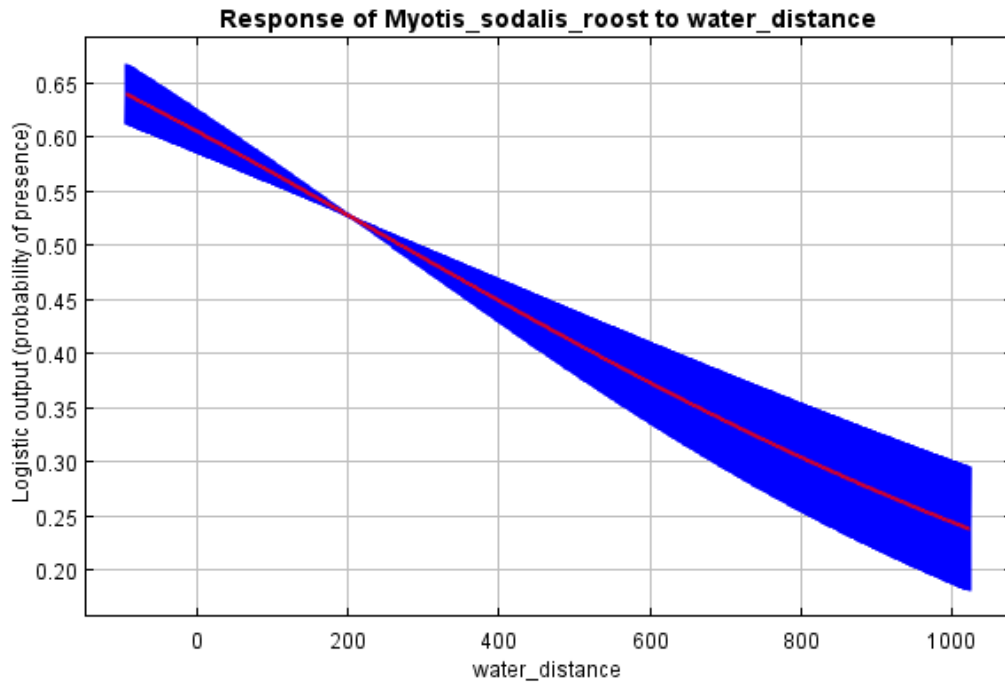


Figure 15. Response Curve for the Distance to Stream Variable (Linear). Distance is calculated in meters.

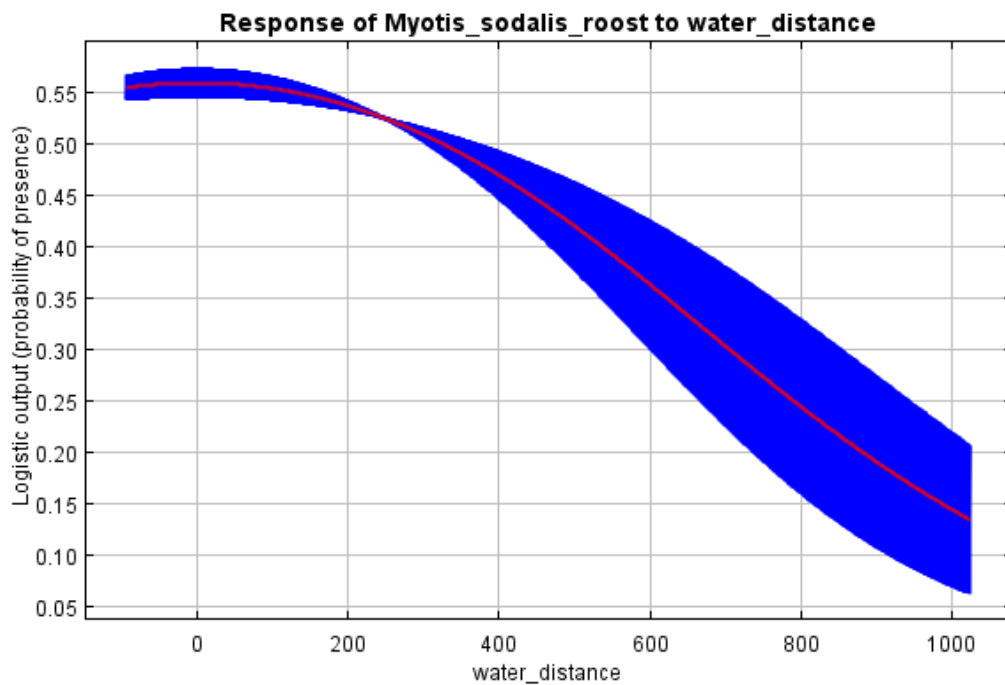


Figure 16. Response Curve for the Distance to Stream Variable (Quadratic). Distance is calculated in meters.

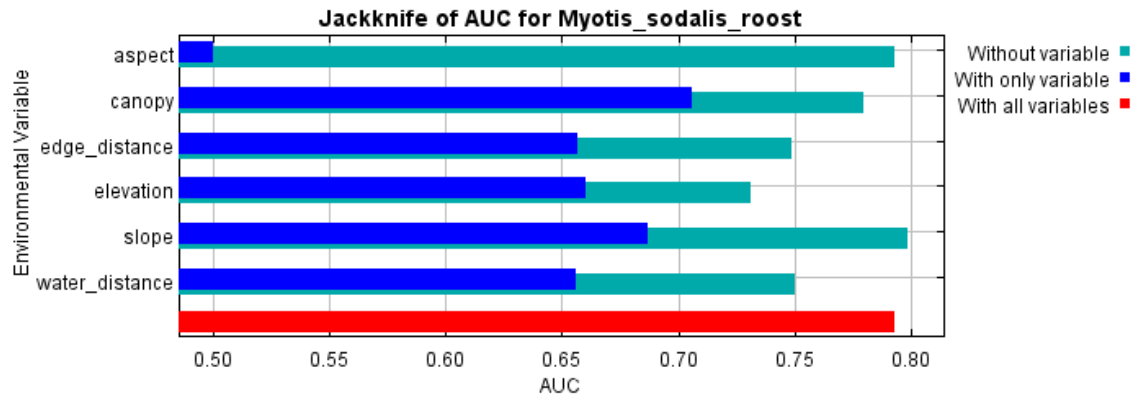


Figure 17. Results of the Jackknife Test Using AUC on Test Data (Linear).

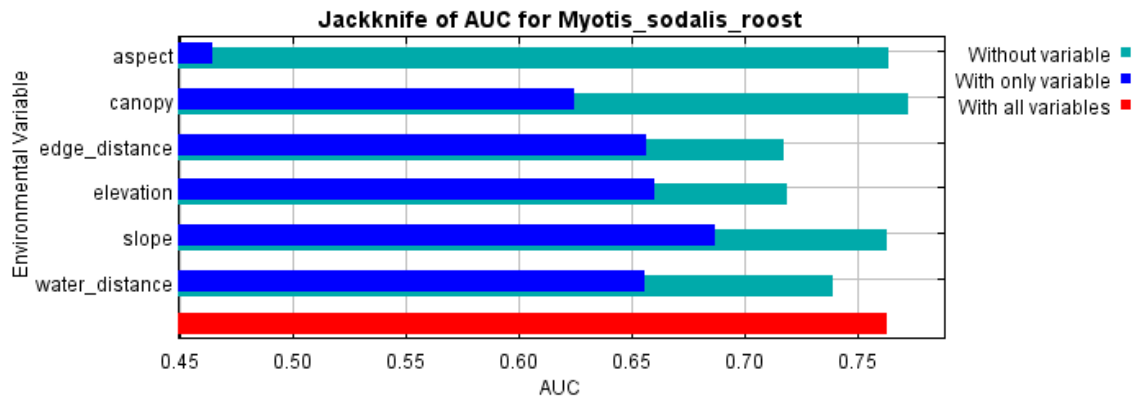


Figure 18. Results of the Jackknife Test Using AUC on Test Data (Quadratic).

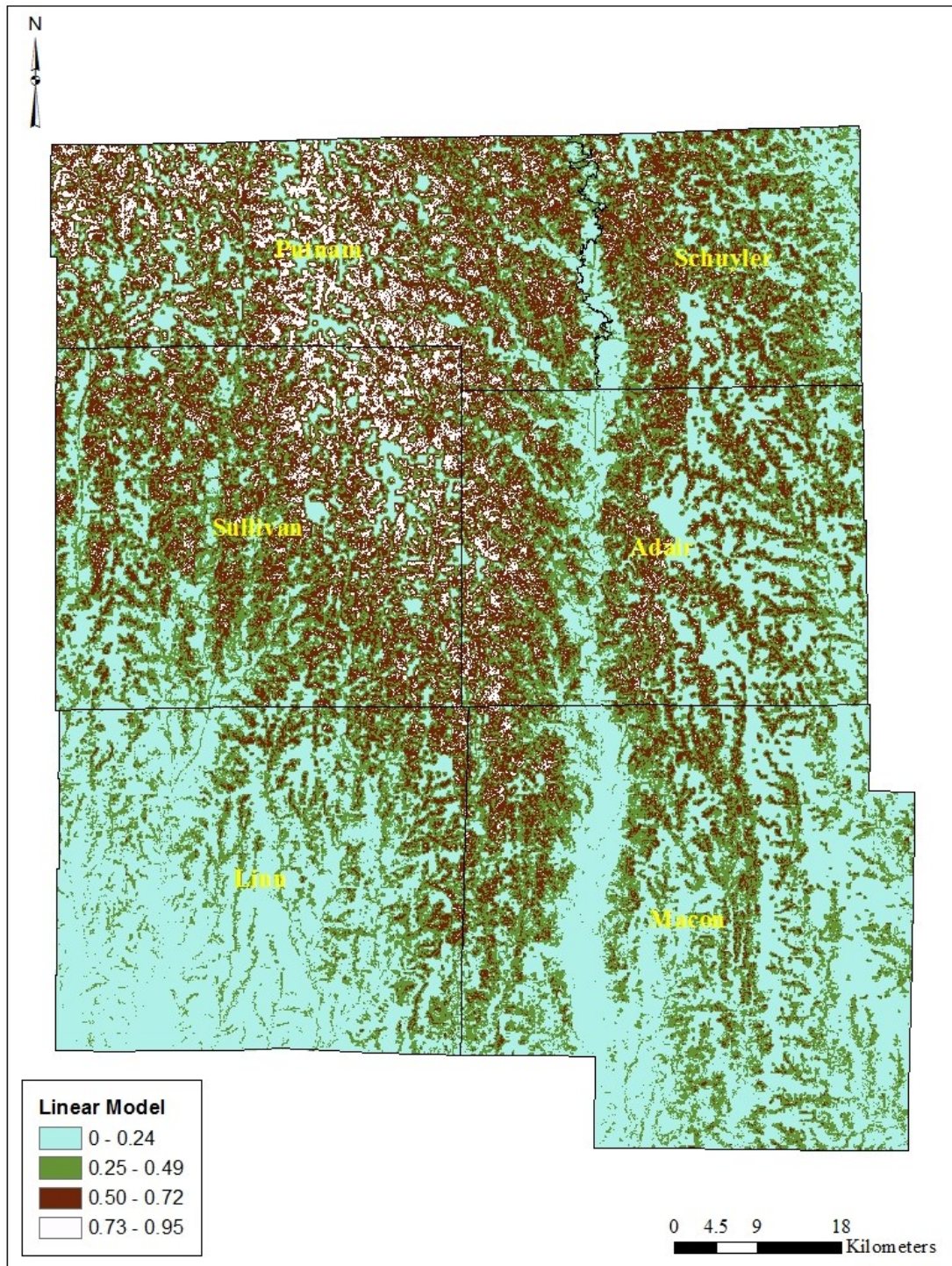


Figure 19. Predictive Map of Indiana Bat Maternity Roost Habitat (Linear). This map shows the probability of occurrence, in percentage, for Indiana bat roost trees for each 30m pixel across the study area.

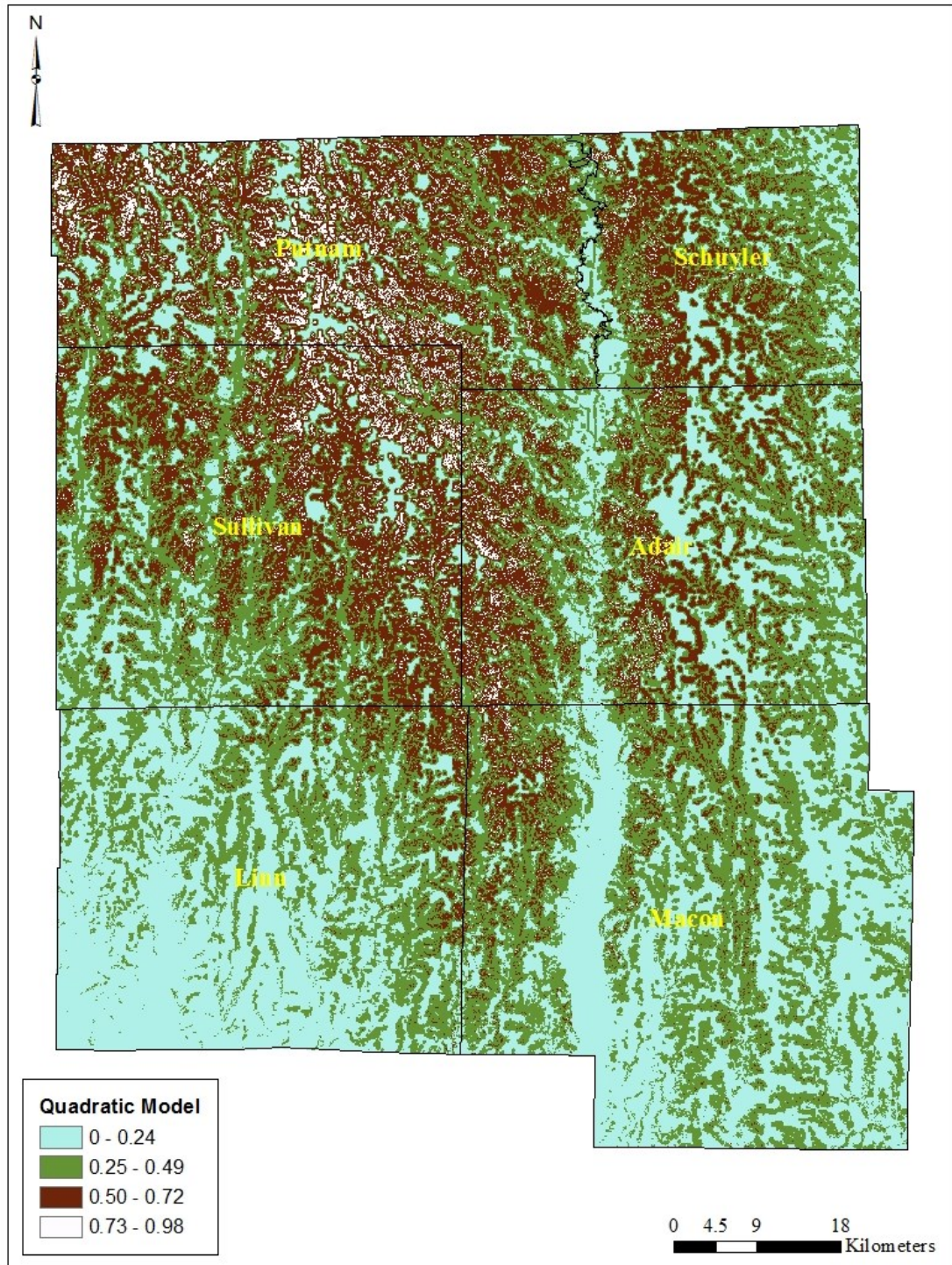


Figure 20. Predictive Map of Indiana Bat Maternity Roost Habitat (Quadratic). This map shows the probability of occurrence, in percentage, for Indiana bat roost trees for each 30m pixel across the study area.